Chapter 7

ZOOPLANKTON

7.1 INTRODUCTION

Zooplankton are included in water quality models primarily because of their effects on algae and nutrients. Algal dynamics and zooplankton dynamics are closely tied through predator-prey interactions. Nutrient dynamics are also influenced by zooplankton since zooplankton excretion is an important component of nutrient recycling, and because of the effects zooplankton have on algal dynamics. These interrelationships are particularly important for long-term simulations in lakes and estuaries since both zooplankton and algal densities may change by orders of magnitude over periods of several months.

As with phytoplankton, zooplankton have been modeled both as a single constituent representing total zooplankton and as several functional groups. The functional groups may represent different feeding types (e.g., herbivores, carnivores, omnivores, non-selective filter feeders, selective filter feeders, etc.) or different taxonomic groups (cladocerans, copepods, rotifers, etc.). While many models use only one group, multiple-group models more realistically represent trophic interactions since, for example, herbivorous zooplankton can be distinguished from carnivorous species. However, multi-group models require more coefficients and model parameters, as well as more detailed information for model calibration.

Zooplankton dynamics are governed by the same general processes as phytoplankton: growth, respiration and excretion, predation, and nonpredatory mortality. The major difference is that zooplankton are not subject to settling losses since they are motile and migrate vertically in the water column, typically in a diurnal pattern. As a result, zooplankton

are usually simulated using the same types of equations and formulations as used for phytoplankton. The general zooplankton equation which forms the basis of almost all models is:

$$\frac{dZ}{dt} = (g_z - r_z - m_z) Z - G_z \tag{7-1}$$

where Z = zooplankton biomass or equivalent nutrient mass, mass or mass/volume

g_z = gross growth rate, 1/time

r_z = respiration and excretion rate, 1/time

m_z = nonpredatory mortality rate, 1/time

G_z = loss rate due to predation, mass/time or mass/volume-time

The above equation treats zooplankton populations as a biomass pool. Zooplankton population models have also been developed which partition the population into a series of age classes, including all important developmental stages from eggs to adults. Growth, respiration, mortality, and reproduction are computed separately for each life stage. Both changes in numbers and changes in the average weights of each age class are typically included in the model structure. While this approach may give a more realistic representation of zooplankton population dynamics, it is generally too detailed to be used in general water quality modeling. As a result, most models use the biomass pool approach, both because it is simpler and because it is consistent with the phytoplankton and nutrient formulations typically used.

As with phytoplankton models, the major differences between zooplankton models are the number of zooplankton groups, the formulations used for each process, and the way in which various processes are combined. Some of these features are compared in Table 7-1 for several zooplankton models. Process formulations are discussed in the following sections.

7.2 TEMPERATURE EFFECTS

Most models include temperature response relationships for essentially all processes affecting zooplankton. Growth, consumption, respiration, and

TABLE 7-1. GENERAL COMPARISON OF ZOOPLANKTON MODELS

Model (Author)	Number of Groups			Zooplankton Processes Computed Separately in Model				Zooplankton Units			Reference
	Zoo-plankton	Phyto-plankton	Fish	Growth	Respiration	Nonpredatory Mortality	Predatory Mortality	Dry Wt. Biomass	Carbon	Other Nutrient	
AQUA-IV	1	1		X	X	X			X		Baca & Arnett (1976)
CE-QUAL-R1	1	2	3	X	X	X	X	X			WES (EWQOS) (1982)
CLEAN	3	2	3	X	X	X	X	X			Bloomfield et al. (1973)
CLEANER	3	3	3	X	X	X	X	X			Scavia & Park (1976)
MS.CLEANER	5	4	8	X	X	X	X	X			Park et al. (1980)
EAM	3	4	20	X	X	X	X	X			Tetra Tech (1979, 1980)
ESTECO	1	2	3	X	X	X	X	X			Brandes & Masch (1977)
EXPLORE-1	1	1		X	X	X			X		Baca et al. (1973)
HSPF	1	1		X	X	X		X			Johanson et al. (1980)
LAKECO	1	2	3	X	X	X	X	X			Chen & Orlob (1975)
MIT Network	1	1		X	X	X				N	Harleman et al. (1977)
WASP	2	2		X	X	X	X		X		Di Toro et al. (1981)
WQRRS	1	2	3	X	X	X	X	X			Smith (1978)
Bierman	2	5		X	X	X		X			Bierman et al. (1980)
Canale	9	4		X	X	X	X		X		Canale et al. (1975, 1976)
Jorgensen	1	1	1	X	X	X	X	X			Jorgensen (1976)
Scavia	6	5		X	X	X	X		X		Scavia et al. (1976)

nonpredatory mortality are generally direct functions of temperature, and predation is indirectly related through temperature effects on the consumption rates of zooplankton predators. In most models, the temperature response formulations used for zooplankton are identical to those used for phytoplankton, and the same temperature function is generally used for all processes affecting a given zooplankton group. The major differences in the response functions between different organisms are the particular coefficient values used to define the shapes and slopes of the response curves, the optimum temperatures, and the upper and lower lethal limits. A few models use different formulations for each process. For example, CE-QUAL-R1 (WES, 1982) uses an optimum curve for growth, a logistic equation for respiration, and a reverse logistic equation for nonpredatory mortality.

The various formulations used to define temperature effects are described in detail in the algal growth section of the report (Section 6.3.1), and they will not be repeated here. In general, all formulations can be classified as either linear response curves, exponential response curves, or temperature optimum curves which exhibit maximum process rates at the optimum temperature and decreasing rates as the temperature moves away from the optimum.

7.3 GROWTH

Zooplankton growth formulations represent increases in the biomass of the population due to both reproduction and the growth of individuals. The growth rate depends on the amount of food which is ingested and assimilated, and is therefore a function of food densities, ingestion rates, and assimilation efficiencies. Part of the assimilated food goes into individual growth and metabolic losses, and part goes into reproduction.

Both ingestion rates and assimilation efficiencies vary according to many factors, including (Leidy and Ploskey, 1980):

- Zooplankton factors such as species, age, size, feeding type, sex, reproductive state, and physiological or nutritional state

- Food related factors such as food concentration, type, particle size, quality, and desirability of the food

- Temperature

Ingestion rates also vary on a diurnal basis, with maximum feeding rates typically occurring at night. Peak nighttime grazing rates have been shown to range from 2 to 27 times the minimum daytime rates (Leidy and Ploskey, 1980).

Almost all zooplankton growth formulations are based on the following fundamental relationship:

$$g_z = C_g E \qquad (7-2)$$

where g_z = zooplankton growth rate, 1/time
C_g = ingestion or grazing rate, mass food/mass zooplankton-time
E = assimilation efficiency, fraction

Since most zooplankton are filter feeders, the ingestion rate is often expressed in terms of a volumetric filtration rate multiplied times the total available food concentration. In this case, the above equation becomes:

$$g_z = C_f F_T E \qquad (7-3)$$

where C_f = zooplankton filtration rate, water volume/mass zooplankton-time
F_T = total available food concentration, mass/volume

For raptorial feeders, the previous equation (Equation (7-2)) is generally used.

The simplest growth formulations assume constant filtration rates and assimilation efficiencies (Figure 7-1). For this situation, the growth rate
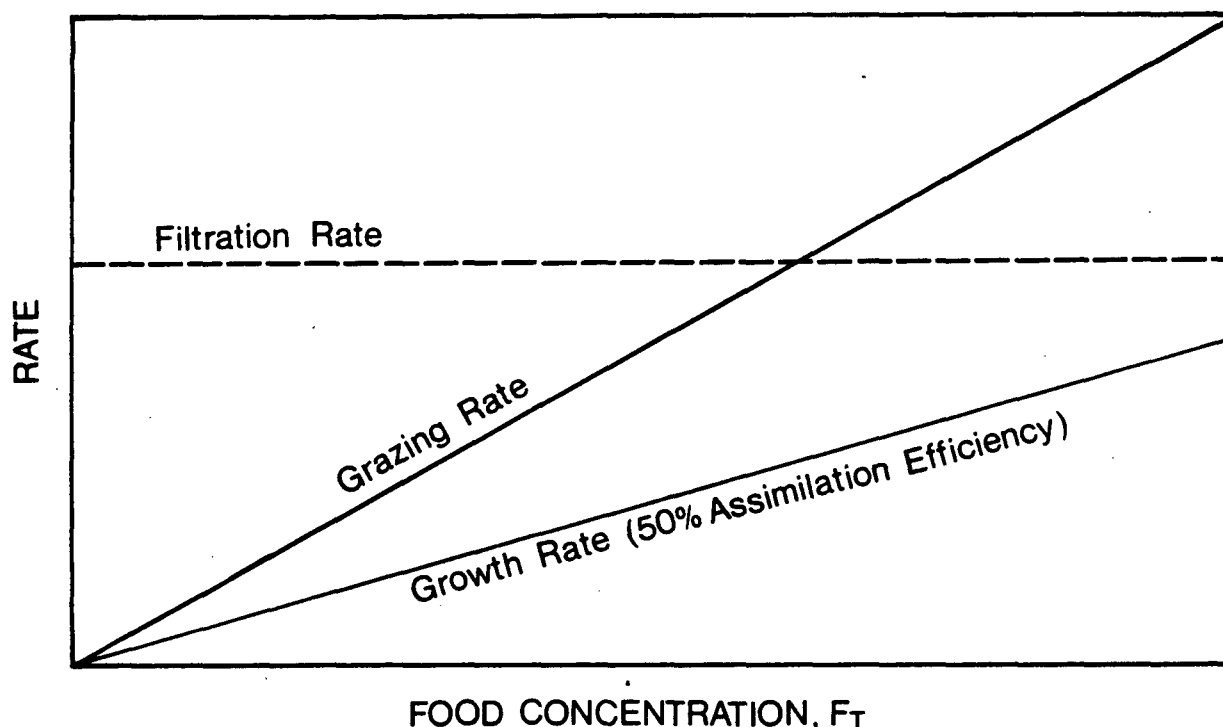
Figure 7-1. Growth rate and grazing rate as a function of food supply for zooplankton with constant filtration rates and assimilation efficiencies (adapted from Leidy and Ploskey, 1980).

is directly proportional to the food supply. More sophisticated models include more complex formulations for the ingestion (or filtration) rates and the assimilation efficiencies to account for variability due to factors like food densities, food types, different feeding methods, and temperature effects on feeding and growth (Canale et al., 1975, 1976; Scavia et al., 1976; Scavia, 1980; Scavia and Park, 1976; Park et al., 1975, 1979, 1980). The effects of food density and temperature on zooplankton growth rates can be expressed in general functional form as:

$$g_z = C_{gmax}(T_{ref}) \, E_{max}(T_{ref}) \, f(T) \, f_g(F_1, F_2, \ldots F_n) \qquad (7\text{-}4)$$

or
$$g_z = C_{fmax}(T_{ref}) \, E_{max}(T_{ref}) \, f(T) \, F_T \, f_f(F_1, F_2, \ldots F_n) \qquad (7\text{-}5)$$

where $C_{gmax}(T_{ref})$ = maximum ingestion rate at reference temperature T_{ref} under conditions of saturated feeding

$$C_{fmax}(T_{ref}) = \text{maximum filtration rate at reference}$$

(excess food supply), mass food/mass zooplankton-time

$C_{fmax}(T_{ref})$ = maximum filtration rate at reference temperature T_{ref}, water volume/mass zooplankton-time

$E_{max}(T_{ref})$ = maximum assimilation efficiency at reference temperature T_{ref}, fraction

$f(T)$ = temperature function for ingestion or filtration and assimilation

$f_g(F_1,F_2,...F_n)$ = growth limitation factor for ingestion formulation (Equation (7-2)) accounting for food density effects on ingestion rates and/or assimilation rates (where $F_1,F_2,...F_n$ are the concentrations of the potential food items)

$f_f(F_1,F_2,...F_n)$ = growth limitation factor for filtration formulation (Equation (7-3)) accounting for food density effects on filtration rates and/or assimilation rates

In some models, the maximum ingestion rate and the maximum assimilation efficiency are combined into a single parameter representing the maximum growth (or assimilation) rate (Chen and Orlob, 1972, 1975; Chen et al., 1975; Jorgensen, 1976; Jorgensen et al., 1978, 1981, 1983; Najarian and Harleman, 1975; Smith, 1978; WES, 1982; Tetra Tech, 1979). In this case, Equation (7-4) becomes:

$$g_z = g_{max}(T_{ref}) \, f(T) \, f_g(F_1,F_2,...F_n) \qquad (7\text{-}6)$$

where $g_{max}(T_{ref})$ = maximum zooplankton growth rate at reference temperature T_{ref}, 1/time

Maximum consumption rates, filtration rates, and growth rates are presented in Tables 7-2, 7-3, and 7-4, respectively.

TABLE 7-2. ZOOPLANKTON MAXIMUM CONSUMPTION RATES

Zooplankton Group	Maximum Consumption Rate (1/day)	References
Total Zooplankton	0.8	Scavia & Park (1976)
	0.35 - 0.50	Bierman (1976)
	0.24 - 1.2**	Collins & Wlosinski (1983)
Omnivores	1.4	Scavia (1980) Bowie et al. (1980)
	0.43	Canale et al. (1976)
Carnivores	1.6	Scavia et al. (1976)
	0.7	Canale et al. (1976)
Fast Ingesters	0.7	Bierman et al. (1980)
Slow Ingesters	0.1	Bierman et al. (1980)
Cladocerans	1.6 - 1.9	Scavia et al. (1976) Scavia (1980) Bowie et al. (1980)
	0.045 - 13.8**	Leidy & Ploskey (1980)
	0.045 - 2.3**	Collins & Wlosinski (1983)
Copeods	1.7 - 1.8	Scavia et al. (1976) Scavia (1980) Bowie et al. (1980)
	0.10 - 0.47**	Collins & Wlosinski (1983)
Rotifers	1.8 - 2.2	Scavia et al. (1976) Scavia (1980) Bowie et al. (1980)
	3.44**	Leidy & Ploskey (1980)
	3.44**	Collins & Wlosinski (1983)
Mysids	1.0 - 1.2	Scavia et al. (1976) Scavia (1980) Bowie et al. (1980)

**Literature values.

TABLE 7-3. ZOOPLANKTON MAXIMUM FILTRATION RATES

Zooplankton Group	Maximum Filtration Rate	Units	References
Total Zooplankton	0.13 - 1.2	1/mgC-day	Di Toro et al. (1971) O'Connor et al. (1975, 1981)
	0.05 - 0.2*	1/mgC-day	Baca & Arnett (1976)
	0.8 - 1.10**	1/mg(D.W.)-day	Di Toro et al. (1971)
Herbivores	0.7 - 1.4	1/mgC-day	Thomann et al. (1975, 1979) Di Toro & Connolly (1980) Di Toro & Matystik (1980) Salisbury et al. (1983)
Carnivores	1.0 - 3.9	1/mgC-day	Thomann et al. (1975, 1979) Di Toro & Connolly (1980) Di Toro & Matystik (1980) Salisbury et al. (1983)
Cladocerans	3.5 - 4.0	1/mg(D.W.)-day	Canale et al. (1976)
	0.2 - 1.6**	1/mg(D.W.)-day	Di Toro et al. (1971)
	0.192 - 0.682**	1/mg(D.W.)-day	Lombardo (1972)
	0.2 - 1.6**	1/mg(D.W.)-day	Jorgensen (1979)
	0.009 - 177**	ml/animal-day	Leidy & Ploskey (1980)
	0.18 - 9.4**	ml/animal-day	Wetzel (1975)
	0.18 - 9.4**	ml/animal-day	Jorgensen (1979)
Copepods	1.0 - 6.5	1/mg(D.W.)-day	Canale et al. (1976)
	0.05 - 2.2**	1/mg(D.W.)-day	Di Toro et al. (1971)
	0.161 - 2.21**	1/mg(D.W.)-day	Lombardo (1972)
	0.05 - 2.2**	1/mg(D.W.)-day	Jorgensen (1979)
	0.02 - 4.1**	ml/animal-day	Wetzel (1975)
	0.02 - 5.28**	ml/animal-day	Jorgensen (1979)
	0.006 - 35.**	ml/animal-day	Leidy & Ploskey (1980)
Rotifers	0.6 - 1.5**	1/mg(D.W.)-day	Di Toro et al. (1971)
	0.6 - 1.5**	ml/animal-day	Jorgensen (1979)
	0.007 - 0.576**	ml/animal-day	Leidy & Ploskey (1980)

*Model documentation values.

**Literature values.

The temperature function f(T) in the above equations uses the same types of formulations discussed previously for phytoplankton. Experimental results suggest optimum type response curves for short term changes in temperature, but more of a linear response curve when acclimation has time to occur (Leidy and Ploskey, 1980). Work by Geller (1975) indicates acclimation times may range from 4 to 6 weeks, which is short enough for zooplankton to acclimate to the typical seasonal variations in temperature, but not to rapid changes (for example, thermal plume effects). However, since feeding is expected to slow down or cease as the temperature approaches the upper lethal limit, an optimum type response curve is appropriate if it is skewed so that the optimum occurs near the upper lethal limit. Table 7-5 presents a comparison of the temperature adjustment functions used in several zooplankton models.

TABLE 7-4. ZOOPLANKTON MAXIMUM GROWTH RATES

Zooplankton Group	Maximum Growth Rate (1/day)	References
Total Zooplankton	0.15 - 0.25	Chen (1970) Chen & Orlob (1975) Chen & Wells (1975, 1976)
	0.175 - 0.2	Jorgensen (1976) Jorgensen et al. (1978)
	0.1 - 0.3*	U.S. Army Corps of Engineers (1974) Brandes (1976) Smith (1978)
	0.15 - 0.30**	Jorgensen (1979)
Cladocerans	0.35 - 0.5	Tetra Tech (1980) Porcella et al. (1983)
	0.27 - 0.74**	Jorgensen (1979)
Copepods	0.5	Tetra Tech (1980)
Rotifers	0.44 - 0.45	Porcella et al. (1983)
	0.24 - 0.76**	Jorgensen (1979)
Mysids	0.14	Tetra Tech (1980)

*Model documentation values.

**Literature values.

Model (Author)	Temperature Formulation (Equation No.)				Reference Temperature	Reference
	Linear	Exponential	Optimum Curve	Other Curve		
AQUA-IV				none		Baca & Arnett (1976)
CE-QUAL-R1			6-24		T_{opt}	WES (EWQOS) (1982)
CLEAN			6-19		T_{opt}	Bloomfield et al. (1973)
CLEANER			6-19		T_{opt}	Scavia & Park (1976)
MS.CLEANER			6-19		T_{opt}	Park et al. (1983)
EAM			6-24		T_{opt}	Tetra Tech (1979, 1980)
ESTECO		6-14			20°C	Brandes & Masch (1977)
EXPLORE-1	X				1°C	Baca et al. (1973)
HSPF		6-14			20°C	Johanson et al. (1980)
LAKECO		6-14			20°C	Chen & Orlob (1975)
MIT Network			6-25		T_{opt}	Harleman et al. (1977)
WASP	X				1°C	Di Toro et al. (1981)
WQRRS			6-24		T_{opt}	Smith (1978)
Bierman		X			20°C	Bierman et al. (1980)
Canale	piecewise linear				1°C	Canale et al. (1975, 1976)
Jorgensen			6-18		T_{opt}	Jorgensen (1976)
Scavia			6-19		T_{opt}	Scavia et al. (1976)

7.3.1 Growth Limitation

The growth limitation functions used in the above equations, $f_g(F_1,F_2,...F_n)$ and $f_f(F_1,F_2,...F_n)$, are somewhat different since the latter function is multiplied times the total available food concentration F_T to give the net grazing rate. Therefore:

$$f_g(F_1,F_2,...F_n) \approx f_f(F_1,F_2,...F_n)\ F_T \qquad (7-7)$$

Both functions typically represent some type of saturation response to feeding, assimilation, and growth. Experimental observations show that at low food concentrations, zooplankton ingestion rates increase with increases in the food supply. For filter feeders which are filtering water at a constant rate, the grazing rate is directly proportional to the food concentration (Figure 7-1). Grazing rates for predatory zooplankton also increase with the food supply at low food concentrations since less energy and time are required to find and capture prey items as the prey density increases. However, as food becomes more abundant, the grazing rates eventually become saturated and level off at some maximum value after which the grazing rate becomes independent of the food supply. Filter feeders can regulate their ingestion rates at high food levels by reducing their filtering rates as the food concentration increases. At low concentrations, the feeding rate is limited by the ability of the zooplankton to filter water, while at high concentrations, it is limited by the ability to ingest and digest the food (Leidy and Ploskey, 1980). Similarly, the feeding rates for carnivorous zooplankton are limited at low prey densities by the ability of the zooplankton to find and capture prey items, while at high prey densities, they are limited by the ability to process, ingest, and digest the prey. Also, at very high ingestion rates, zooplankton growth may be limited by assimilation rates since ingested food remains in the gut for less time, resulting in only partial digestion and reduced assimilation efficiencies.

While the saturation type feeding response has been demonstrated in numerous studies, work by Mayzaud and Poulet (1978) indicates that zooplankton may be able to acclimate to changing food concentrations by adjusting their digestive enzyme levels, allowing them to filter at maximum rates over a much wider range than suggested by the saturation response curves of short term experiments (Leidy and Ploskey, 1980). This results in a linear response curve with ingestion rates directly proportional to the food supply. However, some upper limit on feeding and growth must exist based on theoretical arguments, so a saturation response curve is probably appropriate, even though the saturating food levels may be much higher than

typically experienced in the field except perhaps during phytoplankton blooms.

Two major approaches are used to simulate saturation responses in zooplankton models, the Michaelis-Menten (1913) formulation and the Ivlev (1966) formulation. The Michaelis-Menten formulation is a hyperbolic function analagous to that used in phytoplankton growth calculations, and is probably the most common approach used in water quality models (Chen and Orlob, 1972, 1975; Di Toro and Connolly, 1980; Di Toro and Matystik, 1980; Bloomfield et al., 1973; Park et al., 1974, 1975, 1979, 1980; Scavia et al., 1976; Scavia, 1980; Canale et al., 1975, 1976; Bierman, 1976; Bierman et al., 1980; Baca et al., 1973, 1974; Baca and Arnett, 1976; Najarian and Harleman, 1975). The basic equation is:

$$f_g(F_1, F_2, \ldots F_n) = \frac{F_T}{K_z + F_T} \qquad (7-8)$$

where F_T = total available food supply, mass/volume
K_z = half-saturation constant for zooplankton feeding and growth, mass/volume

The Ivlev formulation is an exponential function which is more popular in biologically oriented models (Kremer and Nixon, 1978). The general equation is:

$$f_g(F_1, F_2, \ldots F_n) = 1 - e^{-K F_T} \qquad (7-9)$$

where K = proportionality constant for Ivlev formulation

Figure 7-2 shows a comparison of the Michaelis-Menten and Ivlev functions where both functions have the same half-saturation value (i.e., $K = -\ln(\frac{1}{2})/K_z$). Both response functions range from minimum values of 0 at very low food concentrations to maximum values of 1 at food saturation. However, for food concentrations below the half-saturation constant (K_z), the Ivlev function is slightly lower than the Michaelis-Menten function.

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For food concentrations above K_z, the Ivlev function is higher and approaches saturation sooner than the Michaelis-Menten function. Note that both functions are used with the total ingestion form of the growth equation (Equation (7-4)) rather than with the filtration form (Equation (7-5)), since the growth limitation function in the filtration form must always be multiplied times the total food supply to get the net response.

Both the Michaelis-Menten and Ivlev formulations can be modified to allow for threshold food concentrations below which zooplankton do not feed. This provides a refuge for prey organisms when they are present in very low concentrations. The resulting equations are:
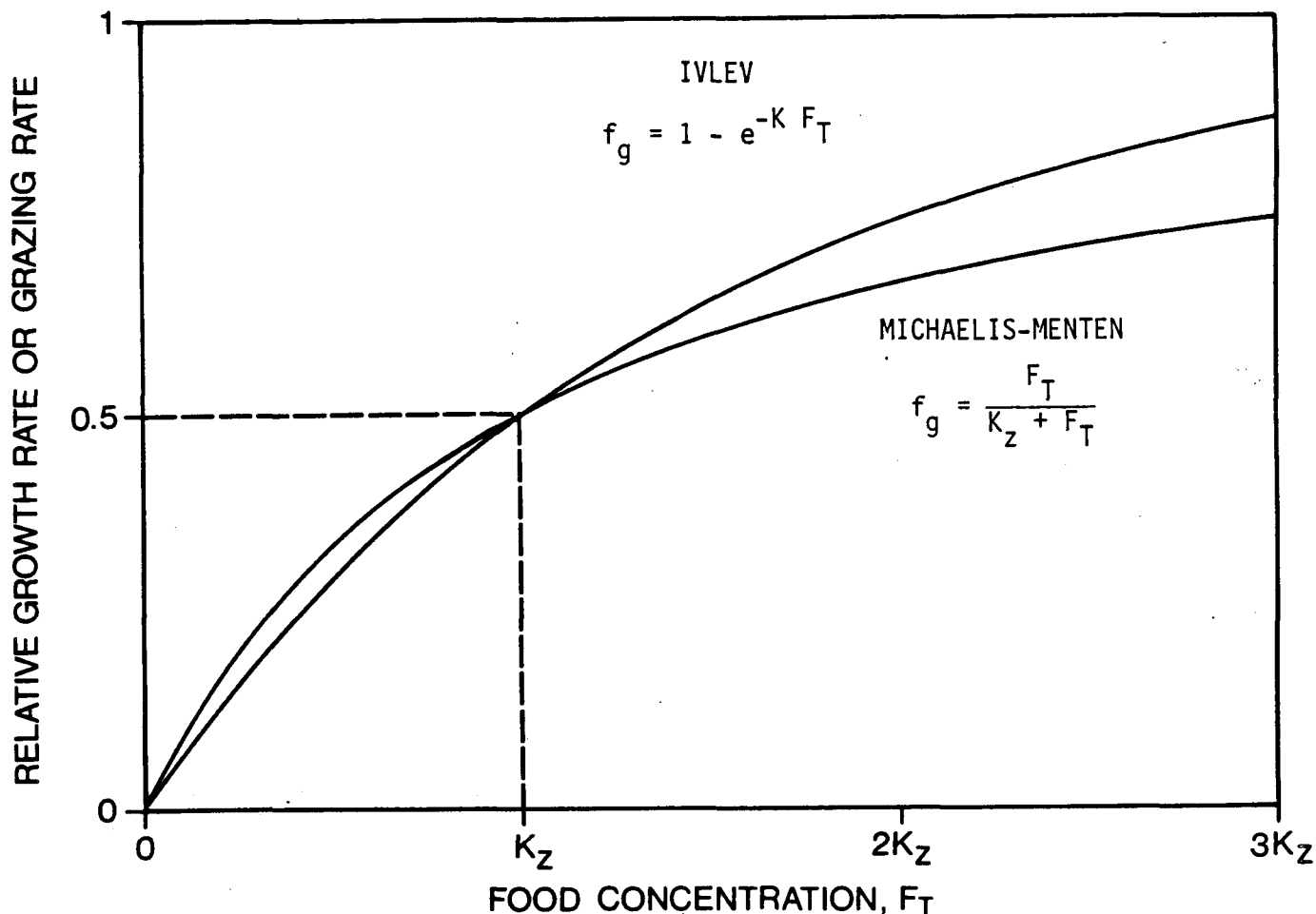

Figure 7-2. Comparison of the Ivlev and Michaelis-Menten functions with the same half-saturation value (i.e., $K = -\ln(\frac{1}{2})/K_z$) (adapted from Swartzman and Bentley, 1977, and Leidy and Ploskey, 1980).

$$f_g(F_1, F_2, \ldots F_n) = \frac{F_T - F_o}{K_z + (F_T - F_o)} \qquad (7\text{-}10)$$

$$f_g(F_1, F_2, \ldots F_n) = \frac{F_T - F_o}{K_z + F_T} \qquad (7\text{-}11)$$

and
$$f_g(F_1, F_2, \ldots F_n) = 1 - e^{-K(F_T - F_o)} \qquad (7\text{-}12)$$

where F_o = threshold food concentration below which feeding does not occur, mass/volume

Zooplankton half-saturation constants and threshold feeding levels are presented in Tables 7-6 and 7-7.

A few models, for example CLEAN, CLEANER, and MS.CLEANER (Bloomfield et al., 1973; Park et al., 1974, 1975, 1979, 1980; Scavia and Park, 1976), use a modified Michaelis-Menten formulation in which the half-saturation constant varies as a function of zooplankton densities to account for competition and feeding interference effects. The equation is:

$$K_z = K_{z1} + K_{z2} Z \qquad (7\text{-}13)$$

where K_{z1} = feeding area coefficient, mass/volume
K_{z2} = competition or interference coefficient

Other saturation response functions besides the Michaelis-Menten and Ivlev formulations have been used in some models. For example, rectilinear saturation curves have been constructed by assuming feeding increases linearly with food concentration until a critical food density is reached, and then levels off at a maximum rate for all concentrations above the critical density. This is expressed as:

$$f_g(F_1, F_2, \ldots F_n) = \frac{F_T}{F_{sat}} \qquad \text{for } F_T < F_{sat} \qquad (7\text{-}14)$$

$$= 1 \qquad \text{for } F_T \geq F_{sat}$$

TABLE 7-6. MICHAELIS-MENTEN HALF-SATURATION CONSTANTS FOR ZOOPLANKTON CONSUMPTION AND GROWTH

Zooplankton Group	Half-Saturation Constant***	Units	References
Total Zooplankton	0.010 - 0.060	mg(Chl a)/l	Di Toro et al. (1971) O'Connor et al. (1975, 1981)
	0.5 (growth)	mg/l	Chen (1970) Chen & Orlob (1975) Chen & Wells (1975, 1976)
	0.5 - 2.0	mg/l	Jorgensen (1976) Jorgensen et al. (1978)
	1.0	mg/l	Bierman et al. (1980)
	0.2 - 0.6* (growth)	mg/l	U.S. Army Corps of Engineers (1974) Brandes (1976) Smith (1978)
	0.06 - 0.6*	mg/l	Baca & Arnett (1976)
Herbivores	0.010 - 0.015	mg(Chl a)/l	Thomann et al. (1975, 1979) Di Toro & Connolly (1980) Di Toro & Matystik (1980) Salisbury et al. (1983)
Carnivores	0.010	mg(Chl a)/l	Thomann et al. (1975)
	0.02	mgC/l	Scavia et al. (1976)
	0.2	mgC/l	Canale et al (1976)
Omnivores	0.2	mgC/l	Canale et al. (1976)
	0.15	mgC/l	Scavia (1980)
	0.375	mg/l	Bowie et al. (1980)
Cladocerans	0.16 - 0.2	mgC/l	Scavia et al. (1976) Scavia (1980)
	0.5	mg/l	Bowie et al. (1980)
	0.8 (growth)	mg/l	Tetra Tech (1980)
	1.8 (growth)	mg/l	Porcella et al. (1983)
Copepods	0.16 - 0.4	mgC/l	Scavia et al. (1976) Scavia (1980)
	1.0	mg/l	Bowie et al. (1980)
	1.2 (growth)	mg/l	Tetra Tech (1980)
Rotifers	0.2 - 0.6	mgC/l	Scavia et al. (1976) Scavia (1980)

TABLE 7-6. (continued)

Zooplankton Group	Half-Saturation Constant***	Units	References
	0.5	mg/1	Bowie et al. (1980)
	2.0 (growth)	mg/1	Porcella et al. (1983)
Mysids	0.10 - 0.20	mgC/1	Scavia et al. (1976) Scavia (1980)
	0.5	mg/1	Bowie et al. (1980)
	2.0 (growth)	mg/1	Tetra Tech (1980)

*Model documentation values.

***Half-saturation constants are for consumption unless specified for growth.

where F_{sat} = food concentration when feeding saturation occurs, mass/volume

or

$$f_g(F_1, F_2, \ldots F_n) = \frac{F_T - F_o}{F_{sat} - F_o} \quad \text{for } F_T < F_{sat} \qquad (7\text{-}15)$$

$$= 1 \quad \text{for } F_T \geq F_{sat}$$

when a threshold feeding concentration F_o is used.

The growth limitation functions used with the filtration form of the growth equation (Equation (7-5)) are different than the saturation response functions discussed above since they must be multiplied by the available food concentration to get the total response. In contrast to the previous functions, these functions generally decrease with increases in the food supply to account for factors like reduced filtering rates, adjustments in particle size selectivity, and reduced assimilation efficiencies which occur at high food concentrations. These types of functions generally have maximum values of 1 at low food densities and decrease assymptotically toward some minimum value as the food density increases.

Di Toro and Matystik (1980) and Di Toro and Connolly (1980) use a reverse Michaelis-Menten formulation to simulate reductions in filtration rates as food concentration increases:

$$f_f(F_1, F_2, \ldots F_n) = 1 - \frac{F_T}{F_T + K_f} \qquad (7\text{-}16)$$

$$= \frac{K_f}{F_T + K_f}$$

where K_f = food concentration at which the filtration rate is 1/2 of its maximum value, mass/volume

TABLE 7-7. THRESHOLD FEEDING LEVELS FOR ZOOPLANKTON

Zooplankton Group	Threshold Feeding Level	References
Total Zooplankton	0.028 mg/1	Scavia & Park (1976)
	0.01 mg/1	Youngberg (1977)
	0.20 mg/1	Bierman et al. (1980)
Carnivores	0.01 mgC/1	Scavia et al. (1976)
Omnivores	0.001 mgC/1	Scavia (1980)
	0.025 mg/1	Bowie et al. (1980)
Cladocerans	0.02 - 0.05 mgC/1	Scavia et al. (1976) Scavia (1980)
	0.05 mg/1	Bowie et al. (1980)
Copepods	0.02 - 0.05 mgC/1	Scavia et al. (1976) Scavia (1980)
	0.05 mg/1	Bowie et al. (1980)
Rotifers	0.02 - 0.05 mgC/1	Scavia et al. (1976) Scavia (1980)
	0.05 mg/1	Bowie et al. (1980)
Mysids	0.02 - 0.05 mgC/1	Scavia et al. (1976) Scavia (1980)
	0.05 mg/1	Bowie et al. (1980)

This function approaches 0 assymptotically at high food densities, resulting in a saturation response for total consumption (Figure 7-3a).

Canale et al. (1975, 1976) use a slightly different formulation to account for reductions in filtering rates and changes in particle size selectivity at high food levels:

$$f_f(F_1, F_2, \ldots F_n) = \frac{K_1 F_T + K_2}{F_T + K_2} \tag{7-17}$$

where K_1 = multiplier for minimum filtering rate (minimum value of f_f)

K_2 = food concentration at which the filtering rate is half way between its minimum and maximum value,

$f_f = 1/2 \ (K_1 + 1)$, mass/volume

This function approaches K_1 assymptotically at high food levels rather than 0. As a result, the total consumption rate continues to increase in proportion to the food supply at high food concentrations since the volumetric filtration rate remains at a constant minimum level (Figure 7-3b). However, a saturation type response can be generated by setting the minimum multiplier K_1 equal to 0, in which case this formulation is identical to Equation (7-16).

A reverse Michaelis-Menten formulation has also been used to simulate reductions in the assimilation efficiencies of filter feeders at high food concentrations (Di Toro et al., 1971, 1977; Di Toro and Matystik, 1980; Di Toro and Connolly, 1980; Thomann et al., 1975, 1979; Canale et al., 1975, 1976). The equation is:

$$f_f(F_1, F_2, \ldots F_n) = \frac{K_a}{F_T + K_a} \tag{7-18}$$

where K_a = food concentration at which the assimilation efficiency is 1/2 of its maximum value, mass/volume
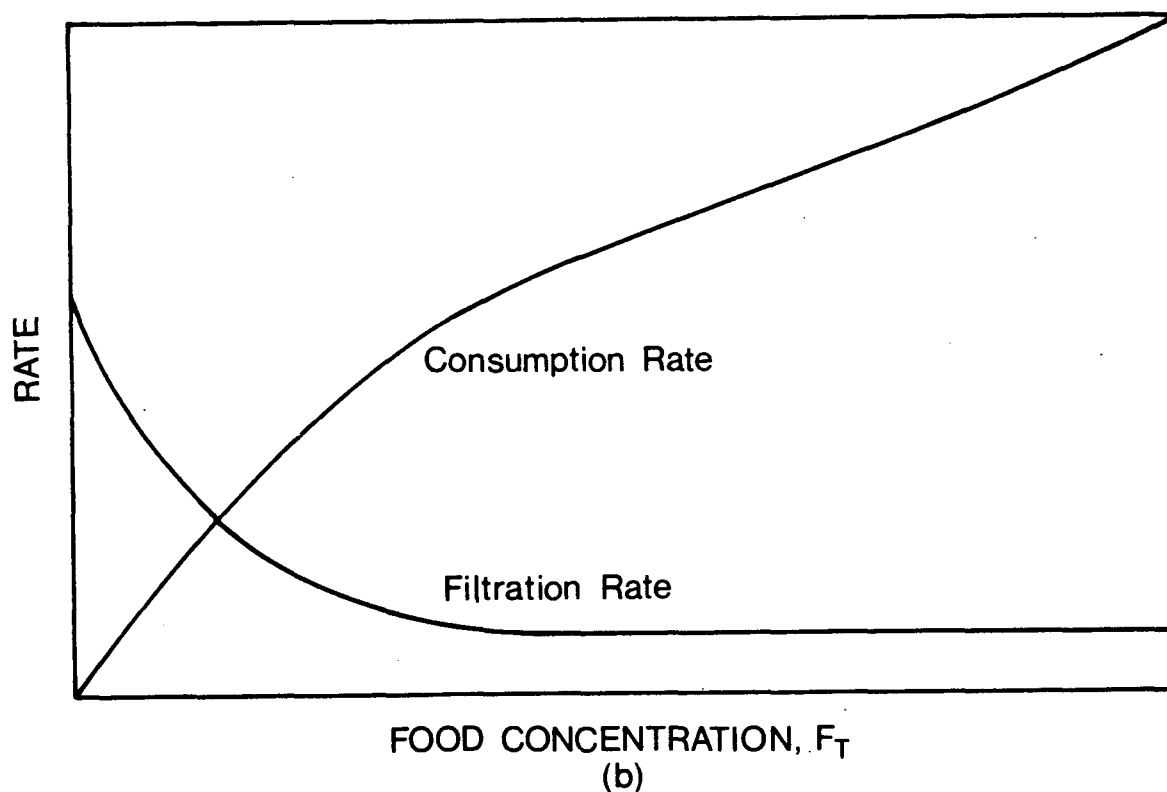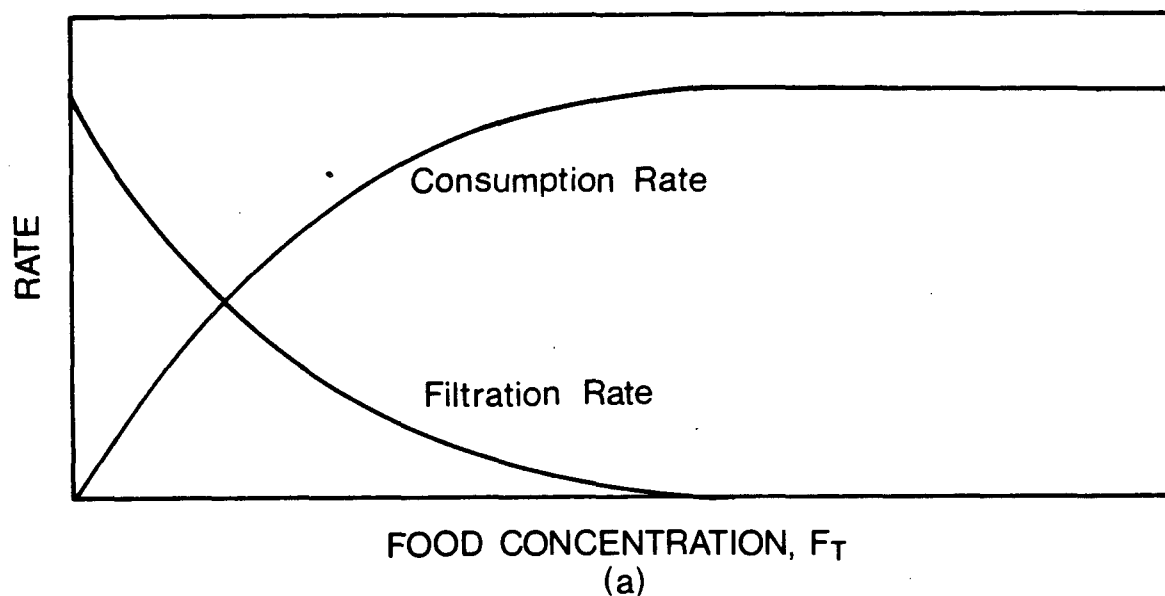
Figure 7-3. Comparison of reverse Michaelis-Menten formulation (a) and Canale et al.'s (1975, 1976) formulation (b) for filtration rate as a function of food concentration.

If a constant volumetric filtration rate is used (Di Toro et al., 1971, 1977; Canale et al., 1975, 1976), this results in a Michaelis-Menten type relationship for total consumption in which the maximum assimilation rate (growth rate) equals the product of the constant filtration rate, maximum assimilation efficiency, and the food concentration at half-maximum assimilation efficiency K_a (ignoring temperature effects):

$$g_z = C_{fmax} E_{max} F_T \left(\frac{K_a}{F_T + K_a} \right)$$

$$= C_{fmax} E_{max} K_a \left(\frac{F_T}{K_a + F_T} \right) \qquad (7\text{-}19)$$

However, Di Toro and Matystik (1980) and Di Toro and Connolly (1980) also use this formulation with a reverse Michaelis-Menten formulation for the filtration rate, which results in a more complicated expression for total consumption involving the product of a Michaelis-Menten term and a reverse Michaelis-Menten term:

$$g_z = C_{fmax} E_{max} K_a \left(\frac{F_T}{K_a + F_T} \right) \left(\frac{K_f}{K_f + F_T} \right) \qquad (7\text{-}20)$$

Zooplankton growth and consumption formulations are compared for several models in Table 7-8.

7.3.2 Food Supply

The total available food concentration F_T used in all of the above growth formulations can be defined in several ways. The simplest approach is to assume all potential food items can be consumed with equal efficiency and define F_T as the sum of the available food concentrations:

$$F_T = \sum_{k=1}^{n} F_K \qquad (7\text{-}21)$$

TABLE 7-8. COMPARISON OF ZOOPLANKTON GROWTH FORMULATIONS

Model (Author)	Food Sources Phyto-plankton	Detritus	Zoo-plankton	Preference Factors Used	Basic Approach Growth Computed Directly	Total Ingestion Computed	Filtration Rate Computed	Growth Limitation Formulation Michaelis-Menten	Ivlev	Variable Assimilation Efficiency	Variable Filtration Rate	Threshold Feeding Included	Assimilation Efficiency Constant	Varies with Food Type	Varies with Food Conc.
AQUA-IV	1					X		X					X		
CE-QUAL-R1	2	1		X		X		X					X		
CLEAN	2	1	3	X		X		X				X		X	
CLEANER	3	1	3	X		X		X				X		X	
MS.CLEANER	4	2	5	X		raptorial feeders	filter feeders	raptors & saturation filterers		X*		X		X	
EAM	4	1	3	X				X					X		
ESTECO	2	1		X	X			X					X		
EXPLORE-1	1					X		X					X		
HSPF	1						X			X					X
LAKECO	2	1		X				X					X		
MIT Network	1				X			X					X		
WASP	2		1				X			X	X				X
WQRRS	2	1		X	X			X					X		
Bierman	5			X		X		X				X	X		
Canale	4		9	X		carnivores	filter feeders	carnivores		nonselective filterers	selective filterers		carnivores & selective filterers		nonselective filterers
Jorgensen	1				X			X				X	X		
Scavia	5	1	6	X		X		X				X		X	

*Maximum assimilation rate used for constant rate filters, with excess consumption egested as pseudofeces.

where F_k = concentration of potential food item k, mass/volume

   n = total number of potential food items

A more realistic approach recognizes that food items vary in the efficiency and frequency at which they are utilized by zooplankton, even if all food items are present in equal concentrations. This is due to factors such as food particle size and shape, desirability and quality of different types of food, ease of capture, and zooplankton feeding behavior. For example, many filter feeders are able to selectively filter different food items with different efficiencies, varying their selectivity according to the abundance and desirability of the various food items present. Food particle shape and size are important distinguishing features since, for example, filamentous algae are often actively rejected or avoided while individual cells of the same species in suspension may be consumed (Leidy and Ploskey, 1980). However, the quality and desirability of the food are also important, since senescent cells are less likely to be consumed than healthy cells of the same species. For raptorial feeders, particle size and shape are not quite as critical since they are able to tear large prey items into smaller pieces before consuming them. Prey desirability and ease of capture then become more important.

The above factors are accounted for in models by assigning feeding preference factors to each potential food item. Preference factors can have values ranging from 1 to 0, with 1 corresponding to a food item which is desirable and easily captured and consumed (or filtered), and 0 corresponding to a food item which is never consumed. Food preference factors have been called selectivity coefficients, electivities, ingestion efficiencies, and several other names in different models, but they all basically represent the same thing--weighting factors which reflect the probability that a given food item will be consumed relative to the others when all foods are present in equal concentrations. They account for the fact that some food items may be less available for consumption than indicated by their concentrations alone. When food preference factors are specified, the total available food concentration F_T is defined as:

$$F_T = \sum_{k=1}^{n} P_k F_k \qquad (7\text{-}22)$$

where P_k = food preference factor for food item k

F_k = concentration of food item K, mass/volume

n = total number of potential food items

Vanderploeg and Scavia (1979) show how preference factors can be derived from the different forms of data reported in zooplankton feeding experiments. In field situations, preference factors may change as the composition of the food supply changes. However, this level of sophistication is generally not included in current ecological models.

7.3.3 Assimilation Efficiencies

In addition to differences in food preferences or ingestion efficiencies for different food types, food items may also differ in their assimilation efficiency by zooplankton. The assimilation efficiencies for different food types varies with the energy content, digestibility, and quality of the food (Leidy and Ploskey, 1980). For example, the assimilation efficiencies for algae are typically higher than for detritus and bacteria, although the assimilation efficiencies for blue-green algae are also generally low. Algae with gelatinous sheaths or resistant cell walls and masses of colonial cells may pass through a zooplankton gut intact and in viable condition (Wetzel, 1975), indicating minimal assimilation efficiencies for these food items. The animal foods of raptorial feeders are assimilated more efficiently than plant foods. Also, since the energy content and digestibility of algae and detritus vary much more widely than animal foods, the assimilation efficiencies for herbivores and detritivores typically cover a much wider range than for carnivorous zooplankton (Leidy and Ploskey, 1980).

Variations in the assimilation efficiencies of different food items can be modeled in several ways. One approach is to incorporate these effects in the food preference factors, for example, by assigning a low value to the preference factor for blue-green algae relative to the other algal groups.

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This in effect lowers the amount of blue-green algae available for zooplankton assimilation and growth. Another approach is to define different maximum assimilation efficiencies for different food items, to compute net assimilation separately for each food item, and then to sum the individual assimilation terms to get the total zooplankton growth rate (Scavia et al., 1976; Scavia, 1980). This can be expressed for the total consumption formulation (Equation (7-4)) as (ignoring temperature effects):

$$g_z = C_{gmax} \sum_{k=1}^{n} \left[E_{max_k} \; f_{g_k}(F_1, F_2, \ldots F_n) \right] \qquad (7-23)$$

where C_{gmax} = maximum total consumption rate, mass food/mass zooplankton-time

E_{max_k} = maximum assimilation efficiency for food item k

$f_{g_k}(F_1, F_2, \ldots F_n)$ = growth limitation factor for food item k

n = total number of potential food items

and for the filtration formulation (Equation (7-5)) as:

$$g_z = C_{fmax} \; f_f(F_1, F_2, \ldots F_n) \sum_{k=1}^{n} \left[E_{max_k} \; P_k \; F_k \right] \qquad (7-24)$$

where C_{fmax} = maximum volumetric filtration, volume/mass zooplankton-time

$f_f(F_1, F_2, \ldots F_n)$ = growth limitation function for filtration formulation

P_k = food preference factor for food item k

F_k = concentration of food item k, mass/volume

Note that growth limitation factors must be computed separately for each food item in the total consumption formulation since the quantities which are summed must reflect both the assimilation efficiencies and the amounts of food consumed for each different food item.

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For the Michaelis-Menten formulation, the individual growth limitation factor may be defined as:

$$f_{g_k}(F_1, F_2, \ldots F_n) = \frac{P_k F_k}{K_z + \sum\limits_{k=1}^{n} P_k F_k} \qquad (7\text{-}25)$$

This is equivalent to the total Michaelis-Menten factor when summed over all food items:

$$\sum_{k=1}^{n} f_{g_k}(F_1, F_2, \ldots F_n) = \sum_{k=1}^{n} \frac{P_k F_k}{K_z + \sum\limits_{k=1}^{n} P_k F_k} = \frac{\sum\limits_{k=1}^{n} P_k F_k}{K_z + \sum\limits_{k=1}^{n} P_k F_k} \qquad (7\text{-}26)$$

Analogous expressions for the Ivlev formulation are more difficult to formulate, since the individual terms are not consistent with the total growth limitation function, even under conditions of equal assimilation efficiencies.

As discussed previously, assimilation efficiencies may decrease with increases in ingestion rate at high food concentrations since the retention time in the gut decreases resulting in incomplete digestion and reduced assimilation. Model formulations to describe these effects have already been discussed in the growth limitation section (Equation (7-18)).

Zooplankton average assimilation efficiencies are presented in Table 7-9. Figures 7-4 and 7-5 present frequency histograms of assimilation efficiency data compiled by Leidy and Plosky (1980).

7.4 RESPIRATION AND MORTALITY

Zooplankton respiration and mortality are modeled using the same general formulations as phytoplankton. Almost all models represent both respiration and nonpredatory mortality rates as either constant coefficients or simple functions of temperature. The basic equations are:

TABLE 7-9. ZOOPLANKTON ASSIMILATION EFFICIENCIES

Zooplankton Group	Assimilation Efficiency	References
Total Zooplankton	0.60 - 0.75	Di Toro et al. (1971) O'Connor et al. (1975, 1981)
	0.63	Jorgensen (1976) Jorgensen et al. (1978)
	0.7	Tetra Tech (1976) Chen & Wells (1975, 1976)
	0.6	Bierman et al. (1980)
	0.5 - 0.8*	Brandes (1976) Smith (1978)
	0.5 - 0.7*	Baca & Arnett (1976)
Herbivores	0.6 (max.)	Thomann et al. (1975, 1979) Di Toro & Connolly (1980) Di Toro & Matystik (1980) Salisbury et al. (1983)
Carnivores	0.6 (max.)	Thomann et al. (1975, 1979) Di Toro & Connolly (1980) Di Toro & Matystik (1980) Salisbury et al. (1983)
	0.5	Scavia et al. (1976)
	0.4 (Cladocerans)	Canale et al. (1976)
Omnivores	0.5 (0.2 for detritus, blue-green algae)	Scavia (1980) Bowie et al. (1980)
	0.4	Canale et al. (1976)
Cladocerans	0.5 (0.2 for detritus, blue-green algae)	Scavia et al. (1976) Scavia (1980) Bowie et al. (1980)
	0.5	Tetra Tech (1980) Porcella et al. (1983)
	0.8 (max.)	Canale et al. (1976)
Copepods	0.5 (0.2 for detritus, blue-green algae)	Scavia et al. (1976) Scavia (1980) Bowie et al. (1980)
	0.7	Canale et al. (1976)

TABLE 7-9. (continued)

Zooplankton Group	Assimilation Efficiency	References
Rotifers	0.5 (0.2 for detritus, blue-green algae)	Scavia et al. (1976) Scavia (1980) Bowie et al. (1980)
	0.5	Tetra Tech (1980) Porcella et al. (1983)
Mysids	0.5 (0.2 for detritus, blue-green algae)	Scavia et al. (1976) Scavia (1980) Bowie et al. (1980)
	0.5	Tetra Tech (1980)

*Model documentation values.

$$r_z = r_z(T_{ref}) \, f_r(T) \qquad (7\text{-}27)$$

and

$$m_z = m_z(T_{ref}) \, f_m(T) \qquad (7\text{-}28)$$

where r_z = zooplankton respiration rate, 1/time

$r_z(T_{ref})$ = respiration rate at reference temperature T_{ref}, 1/time

$f_r(T)$ = temperature function for respiration

m_z = zooplankton nonpredatory mortality rate, 1/time

$m_z(T_{ref})$ = nonpredatory mortality at reference temperature T_{ref}, 1/time

$f_m(T)$ = temperature function for nonpredatory mortality

Since the respiration and nonpredatory mortality rate equations have the same basic form and typically use the same temperature functions, many models combine both processes into a single loss term:

$$r_z + m_z = d_z(T_{ref}) \, f_r(T) \qquad (7\text{-}29)$$

where $d_z(T_{ref})$ = total loss rate due to both respiration and nonpredatory mortality at reference temperature T_{ref}, 1/time
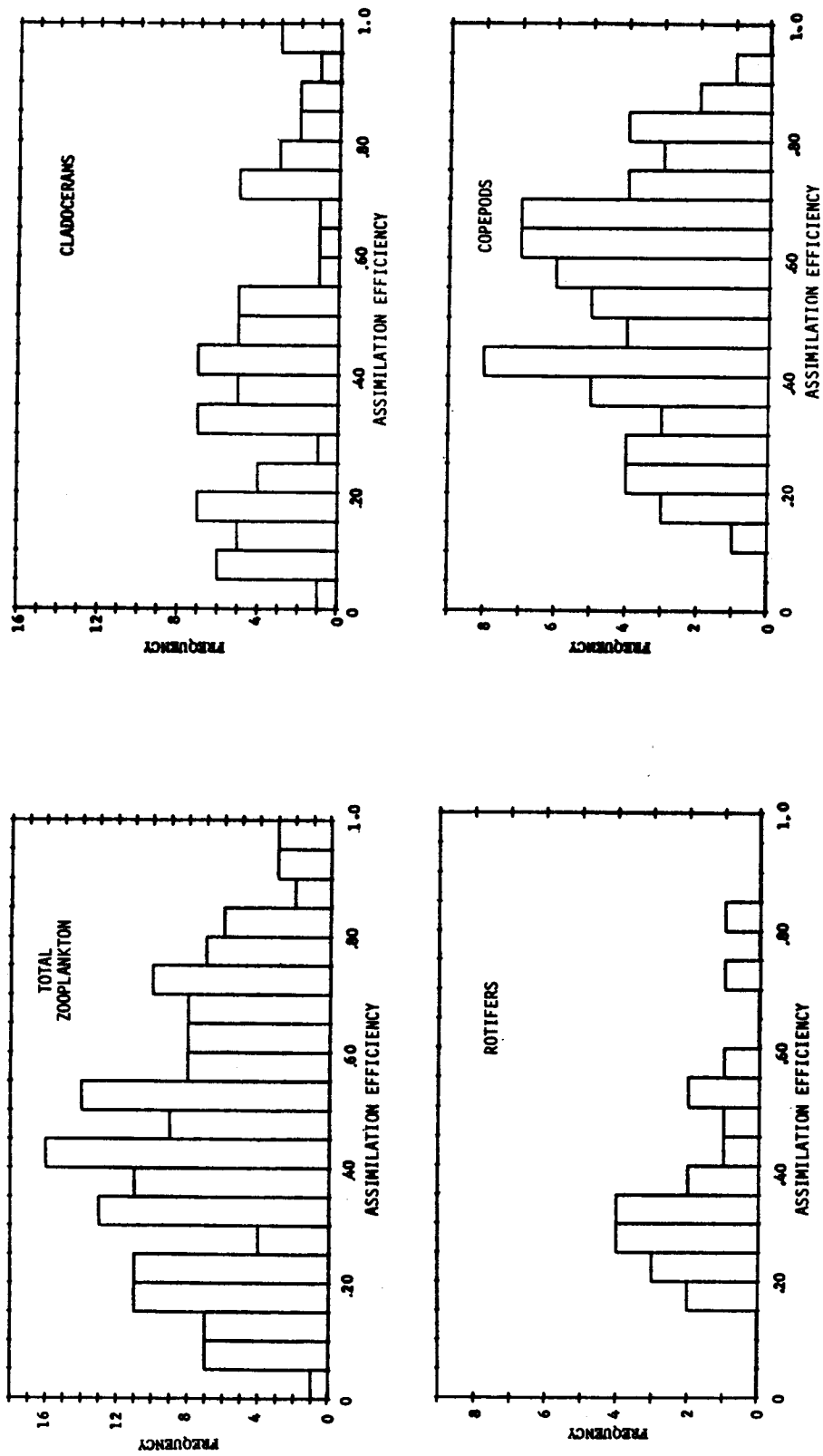
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Figure 7-4. Frequency histograms for zooplankton assimilation efficiencies (from Leidy and Ploskey, 1980).

In a few models, the respiration rate is partitioned into two components, 1) the standard respiration rate representing the combined basal metabolism and digestion energetics and 2) the active respiration rate which represents the additional respiration associated with zooplankton activity. These two components can be distinguished by using different temperature response functions for each component. For example, standard respiration is
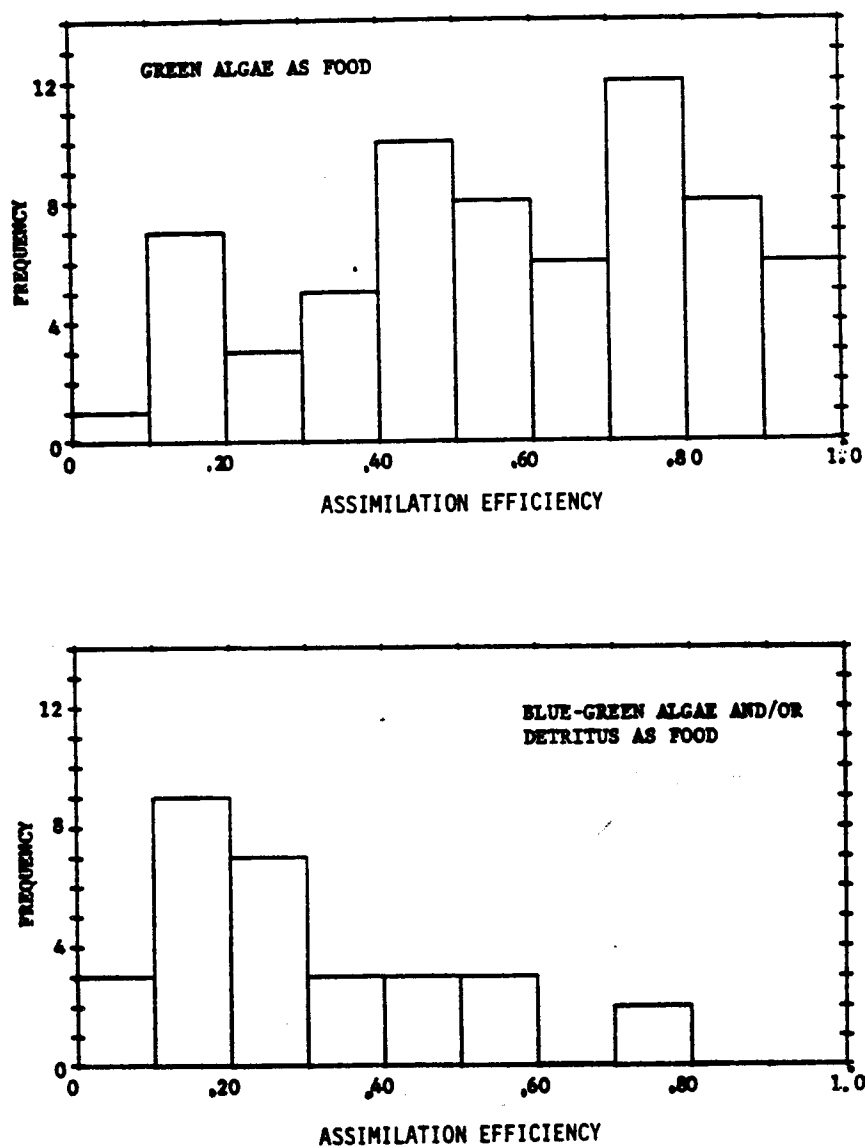

Figure 7-5.   Frequency histograms showing variations in zooplankton assimilation efficiencies with different food types (from Leidy and Ploskey, 1980)

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typically associated with an exponential temperature curve which increases until the upper lethal limit is approached, while the active respiration rate may be associated with a temperature optimum curve:

$$r = r_{std}(T_{ref}) \, f_s(T) + r_{act}(T_{ref}) \, f_a(T) \qquad (7\text{-}30)$$

where $r_{std}(T_{ref})$ = standard respiration rate at reference temperature T_{ref}, 1/day

$f_s(T)$ = temperature function for standard respiration

$r_{act}(T_{ref})$ = active respiration rate at reference temperature T_{ref}, 1/day

$f_a(T)$ = temperature function for active respiration

Another approach is to assume that the activity level (and active respiration) is proportional to the feeding level by using a Michaelis-Menten or Ivlev function:

$$r = r_{std}(T_{ref}) \, f_s(T) + r_{act}(T_{ref}) \, f_a(T) \, f(F_1, F_2, \ldots F_n) \qquad (7\text{-}31)$$

where $f(F_1, F_2, \ldots F_n)$ = growth limitation factor as a function of food supply

This approach is used by Scavia et al. (1976) and Scavia (1980) where the first term represents the minimum endogenous respiration rate under starvation conditions and the second term represents the increase in respiration associated with feeding.

A similar formulation is used in CLEANER (Scavia and Park, 1976) and MS.CLEANER (Park et al., 1979, 1980) where the active respiration rate is expressed as a fraction of the total consumption rate:

$$r = \left[r_{min}(T_{ref}) + K_r \, C_g \right] f(T) \qquad (7\text{-}32)$$

where $r_{min}(T_{ref})$ = minimum endogenous respiration under starvation conditions at reference temperature T_{ref}, 1/time

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K_r = fraction of ingested food which is respired

C_g = ingestion rate, 1/time

The CLEANER and MS.CLEANER models also include additional factors to account for crowding effects and population age effects on both respiration and nonpredatory mortality rates. The crowding factor is expressed as:

$$f_{crd} = 1 + \frac{K_c Z}{Z_{cap}}$$ (7-33)

where f_{crd} = crowding factor

K_c = crowding coefficient

Z_{cap} = zooplankton carrying capacity, mass or mass/volume

This factor increases the respiration and mortality rates as zooplankton density increases. The age factor accounts for the effects of the population age structure on the net respiration and mortality rates since these rates generally vary with age. The basic assumption is that the population consists primarily of immature individuals at low zooplankton densities and of adults at high population densities (Scavia and Park, 1976). The age factor represents the difference between adult and juvenile rates. The age factor for respiration is expressed as:

$$f_{rage} = 1 + K_{rx}\left(\frac{Z_{cap} - Z}{Z_{cap}}\right)$$ (7-34)

where f_{rage} = age factor for respiration

K_{rx} = fractional increase in respiration rate between young zooplankton and adults

and the age factor for mortality is expressed as:

$$f_{mage} = 1 - K_{mx}\left(\frac{Z_{cap} - Z}{Z_{cap}}\right)$$ (7-35)

where f_{mage} = age factor for nonpredatory mortality

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K_{mx} = fractional decrease in mortality rate between young zooplankton and adults

Both the crowding and age structure factors are multiplied with the respiration and nonpredatory mortality rates defined in Equations (7-32) and (7-28) to incorporate these effects into the rates.

Some versions of CLEANER (Youngberg, 1977) also include an oxygen reduction factor in the respiration equation to account for decreases in respiration at low dissolved oxygen levels. The equation is:

$$f_{ox} = \frac{O_2 - O_{min}}{K_{ox} + (O_2 - O_{min})} \qquad (7-36)$$

where f_{ox} = oxygen reduction factor

O_2 = ambient oxygen concentration, mg/l

O_{min} = minimum oxygen requirement, mg/l

K_{ox} = half-saturation constant for oxygen limitation (set at 0.9 mg/l)

Bierman et al. (1980) use a second order formulation for zooplankton mortality when the zooplankton density exceeds a critical level. This accounts for density dependent effects on both natural mortality and predatory mortality (which is not directly simulated in this model) at high densities. The equation is:

$$m = \left[m_1(T_{ref}) + K_m(T_{ref}) \, Z \right] \, f(T) \qquad (7-37)$$

where $m_1(T_{ref})$ = mortality rate below the critical zooplankton density at reference temperature T_{ref}, 1/time

$K_m(T_{ref})$ = density dependent mortality coefficient for increased mortality above the critical zooplankton density at reference temperature T_{ref}, 1/mass zooplankton-time

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The nonpredatory mortality rate can also be partitioned into several components which account for specific types of mortality such as natural senescence, thermally-induced mortality, toxic mortality, and stress-induced mortality due to low dissolved oxygen, pH extremes, starvation, etc. The general equation is:

$$m_z = m_z(T_{ref}) \, f_m(T) + m_T(T_{ref}) \, f_T(T) + m_x(T_{ref}) \, f_1(T) \, f_x(X)$$

$$+ \, m_s(T_{ref}) \, f_2(T) \, f(O_2, pH, \ldots) + m_f(T_{ref}) \, f_3(T) + f_f(F_T) \quad (7\text{-}38)$$

where $m_z(T_{ref})$ = mortality rate due to senescence at reference temperature T_{ref}, 1/time

$f_m(T)$ = temperature function for senescent mortality

$m_T(T_{ref})$ = thermal mortality rate at reference temperature T_{ref}, 1/time

$f_T(T)$ = thermal mortality response curve

$m_x(T_{ref})$ = toxic mortality rate at reference temperature T_{ref}, 1/time

$f_1(T)$ = temperature function for toxic mortality

$f_x(X)$ = dose-response curve for toxic mortality

X = concentration of toxicant, mass/volume

$m_s(T_{ref})$ = stress-induced mortality rate for low dissolved oxygen, pH extremes, etc., at reference temperature T_{ref}, 1/time

$f_2(T)$ = temperature function for stress-induced mortality

$f(O_2, pH \ldots)$ = stress-induced mortality function for low dissolved oxygen, pH extremes, etc.

$m_f(T_{ref})$ = starvation-induced mortality rate at reference temperature T_{ref}, 1/time

$f_3(T)$ = temperature function for starvation mortality

$f_f(F_T)$ = starvation mortality function

Various formulations could be used to define these effects, although most current models deal only with natural mortality and sometimes thermal effects.

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Zooplankton respiration rates and mortality rates are presented in Tables 7-10 and 7-11. Figures 7-6 and 7-7 present frequency histograms of respiration rates and nonpredatory mortality rates from data compiled by Leidy and Ploskey (1980).

7.5 PREDATORY MORTALITY

Zooplankton predatory mortality is modeled using the same formulations described previously for phytoplankton. However, since zooplankton are often the highest trophic level included in water quality models, predator-prey dynamics between zooplankton and higher trophic levels cannot usually be simulated. Therefore, predation by fish and carnivorous zooplankton is modeled by either assuming a constant predation loss which is specified as a model input parameter:

$$G_Z = \text{constant} \tag{7-39}$$

where G_Z = total predatory mortality rate by all zooplankton consumers, mass zooplankton/time

or by assuming a loss rate which is directly proportional to the zooplankton densities:

$$G_Z = e_Z Z \tag{7-40}$$

or
$$G_Z = e_Z(T_{ref}) \, f_e(T) \, Z \tag{7-41}$$

where e_Z = predatory mortality rate coefficient, 1/time

Z = zooplankton biomass or concentration, mass or mass/volume

$e_Z(T_{ref})$ = predatory mortality rate coefficient at reference temperature T_{ref}, 1/time

$f_e(T)$ = temperature function for predatory mortality

Since these formulations are essentially the same as those used for nonpredatory mortality, nonpredatory mortality and predation losses are

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TABLE 7-10. ZOOPLANKTON RESPIRATION RATES

Zooplankton Group	Respiration Rate	Units	Temperature	References
Total Zooplankton	0.01	1/day	20°C	Chen (1970) Chen & Orlob (1975) Chen & Wells (1975, 1976)
	0.02 - 0.035	1/day	20°C	Jorgensen (1976) Jorgensen et al. (1978)
	0.36	1/day	20°C	Lombardo (1972)
	0.02 - 0.16	1/day	20°C	O'Connor et al. (1975)
	0.005 - 0.02	1/day	20°C	Tetra Tech (1976)
	0.001 - 0.11*	1/day	20°C	U.S. Army Corps of Engineers (1974) Brandes (1976) Smith (1978)
	0.005 - 0.3*	1/day	20°C	Baca & Arnett (1976)
Herbivores	0.02 - 0.03	1/day	20°C	Thomann et al. (1975, 1979) Di Toro & Connolly (1980) Di Toro & Matystik (1980) Salisbury et al. (1983)
Carnivores	0.007 - 0.02	1/day	20°C	Thomann et al. (1975, 1979) Di Toro & Connolly (1980) Di Toro & Matystik (1980) Salisbury et al. (1983)
	0.30	1/day	T_{opt}	Scavia et al. (1976)
	0.04 - 0.06	1/day	20°C	Canale et al. (1976)
Omnivores	0.08 - 0.33	1/day	T_{opt}	Scavia (1980) Bowie et al. (1980)
	0.04 - 0.06	1/day	20°C	Canale et al. (1976)
Cladocerans	0.1 - 0.36	1/day	T_{opt}	Scavia et al. (1976) Scavia (1980) Bowie et al. (1980)
	0.017 - 0.10	1/day	20°C	Tetra Tech (1980) Porcella et al. (1983)
	0.04 - 0.06	1/day	20°C	Canale et al. (1976)
	0.157 - 0.413**	1/day	20°C	Lombardo (1972)
	0.090 - 0.216**	1/day	20°C	Leidy & Ploskey (1980)
	0.006 - 0.772**	1/day	T_{opt}	Collins & Wlosinski (1983)
	8.5 - 14.2**	$\dfrac{ml\ O_2}{mg(D.W.)-day}$	18°C	Di Toro et al. (1971)

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TABLE 7-10. (continued)

Zooplankton Group	Respiration Rate	Units	Temperature	References
	5.4 - 14.2**	$\frac{ml\ O_2}{mg(D.W.)-day}$	20°C	Lombardo (1972)
	14.2**	$\frac{ml\ O_2}{mg(D.W.)-day}$	20°C	Jorgensen (1979)
Copepods	0.1 - 0.35	1/day	T_{opt}	Scavia et al. (1976) Scavia (1980) Bowie et al. (1980)
	0.04 - 0.06	1/day	20°C	Canale et al. (1976)
	0.017	1/day	20°C	Tetra Tech (1980)
	0.085 - 0.550**	1/day	20°C	Lombardo (1972)
	0.064 - 0.738**	1/day	20°C	Leidy & Ploskey (1980)
	0.043 - 0.695**	1/day	T_{opt}	Collins & Wlosinski (1983)
	3.0 - 12.2**	$\frac{ml\ O_2}{mg(D.W.)-day}$	20°C	Di Toro et al. (1971)
	2.93 - 18.9**	$\frac{ml\ O_2}{mg(D.W.)-day}$	20°C	Lombardo (1972)
	3.0 - 13.5**	$\frac{ml\ O_2}{mg(D.W.)-day}$	20°C	Jorgensen (1979)
Rotifers	0.12 - 0.40	1/day	T_{opt}	Scavia et al. (1976) Scavia (1980) Bowie et al. (1980)
	0.15	1/day	20°C	Porcella et al. (1983)
	0.163 - 0.677**	1/day	20°C	Leidy & Ploskey (1980)
Mysids	0.05 - 0.28	1/day	T_{opt}	Scavia et al. (1976) Scavia (1980) Bowie et al. (1980)
	0.022	1/day	20°C	Tetra Tech (1980)

*Model documentation values.
**Literature values.

often combined into a single total mortality term when higher trophic levels are not directly simulated:

$$m_{tot} = \left[m_z(T_{ref}) + e_z(T_{ref}) \right] f_m(T) \qquad (7\text{-}42)$$

$$= m_{tot}(T_{ref})\ f_m(T)$$

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where m_{tot} = total mortality rate, 1/time

$m_{tot}(T_{ref})$ = total mortality rate at reference temperature T_{ref}, 1/time

In ecologically oriented models where long term seasonal changes in population dynamics are important, zooplankton are often separated into several functional groups based on general feeding types (filter feeders, carnivorous raptors, omnivores, etc.) or on major taxonomic groups (cladocerans, copepods, rotifers) (Canale et al., 1975, 1976; Scavia et al., 1976; Scavia, 1980; Park et al., 1974, 1975, 1979, 1980; Chen et al., 1975; Tetra Tech, 1979). Although several species must be lumped into each functional group, this approach recognizes the importance of complexities in the food web, different foraging strategies, and predator population dynamics in evaluating both zooplankton and phytoplankton dynamics. Several planktivorous fish groups are also sometimes provided for the same reasons. (Chen et al., 1975; Tetra Tech, 1979; Park et al., 1979, 1980).

In these situations, zooplankton predation rates are computed as the sum of the consumption rates by all potential predators, including carnivorous or omnivorous zooplankton and planktivorous fish. The general relationship for predatory mortality can be expressed as:

$$G_{z_i} = \sum_{j=1}^{n_p} \left[C_j \, X_j \, \frac{P_{ij} \, Z_i}{\sum_{k=1}^{n_j} P_{kj} \, F_{kj}} \right] \tag{7-43}$$

where G_{z_i} = total predatory mortality rate for zooplankton group i, mass zooplankton/time

n_p = total number of zooplankton consumers

C_j = total consumption rate by predator group j, 1/time

X_j = biomass or concentration of predator group j, mass or mass/volume

P_{ij} = food preference factor for predator group j feeding on zooplankton group i

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TABLE 7-11. ZOOPLANKTON MORTALITY RATES

Zooplankton Group	Mortality Rate (1/day)	Mortality Type	References
Total Zooplankton	0.075	total	Di Toro et al. (1971)
	0.125	nonpredatory	Jorgensen (1976)
	0.025 - 0.033	nonpredatory	Jorgensen et al. (1978)
	0.005	nonpredatory	Chen and Wells (1975, 1976)
	0.02	nonpredatory	Tetra Tech (1980)
	0.015	total	O'Connor et al. (1981)
	0.005*	nonpredatory	U.S. Army Corps of Engineers (1974)
	0.001 - 0.005*	nonpredatory	Brandes (1976)
	0.005 - 0.02*	nonpredatory	Smith (1978)
	0.003 - 0.075**	total	Jorgensen (1979)
Carnivores	0.01	nonpredatory	Scavia et al. (1976)
	0.01	fish grazing	Scavia et al. (1976)
Omnivores	0.005	fish grazing	Scavia (1980)
Fast Ingesters	0.05	nonpredatory	Bierman et al. (1980)
Slow Ingesters	0.01	nonpredatory	Bierman et al. (1980)
Cladocerans	0.01	nonpredatory	Scavia et al. (1976)
	0.04 - 0.05	fish grazing	Scavia et al. (1976)
	0.001 - 0.005	fish grazing	Scavia (1980)
	0.01	nonpredatory	Tetra Tech (1980)
	0.1	nonpredatory	Porcella et al. (1983)
	0.0007 - 0.027**	nonpredatory	Leidy & Ploskey (1980)
	0.001 - 0.027**	nonpredatory	Collins & Wlosinski (1983)
Copepods	0.01	nonpredatory	Scavia et al. (1976)
	0.05	fish grazing	Scavia et al. (1976)
	0.002	fish grazing	Scavia (1980)
	0.003 - 0.005	nonpredatory	Canale et al. (1976)
	0.01	nonpredatory	Tetra Tech (1980)

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TABLE 7-11. (continued)

Zooplankton Group	Mortality Rate (1/day)	Mortality Type	References
	0.0005 - 0.153**	nonpredatory	Leidy & Ploskey (1980)
	0.003 - 0.155**	nonpredatory	Collins & Wlosinski (1983)
Rotifers	0.01	nonpredatory	Scavia et al. (1976)
	0.12	nonpredatory	Porcella et al. (1983)
Mysids	0.01	nonpredatory	Scavia et al. (1976)
	0.1	fish grazing	Scavia et al. (1976)
	0.08	fish grazing	Scavia (1980)
	0.01	nonpredatory	Tetra Tech (1980)

*Model documentation values.

**Literature values.

Z_i = biomass or concentration of zooplankton group i, mass or mass/volume

n_j = total number of potential food items for predator group j

P_{kj} = food preference factor for predator group j feeding on food item k

F_{kj} = biomass or concentration of potential food item k consumed by predator group j, mass or mass/volume

The quantity $\left(P_{ij} \, Z_i \middle/ \sum_{k=1}^{n_j} P_{kj} F_{kj}\right)$ in Equation (7-43) represents the fraction of the total food consumption by predator group j which is provided by zooplankton group i. The quantity $C_j X_j$ represents the total rate of food ingestion by predator group j. Ingestion rate formulations for carnivorous zooplankton were discussed in the previous section. Consumption rates for planktivorous fish are generally modeled in the same way. As discussed in the algae chapter, consumption rates are sometimes back-calculated from computed growth rates and known assimilation efficiencies using the equation:
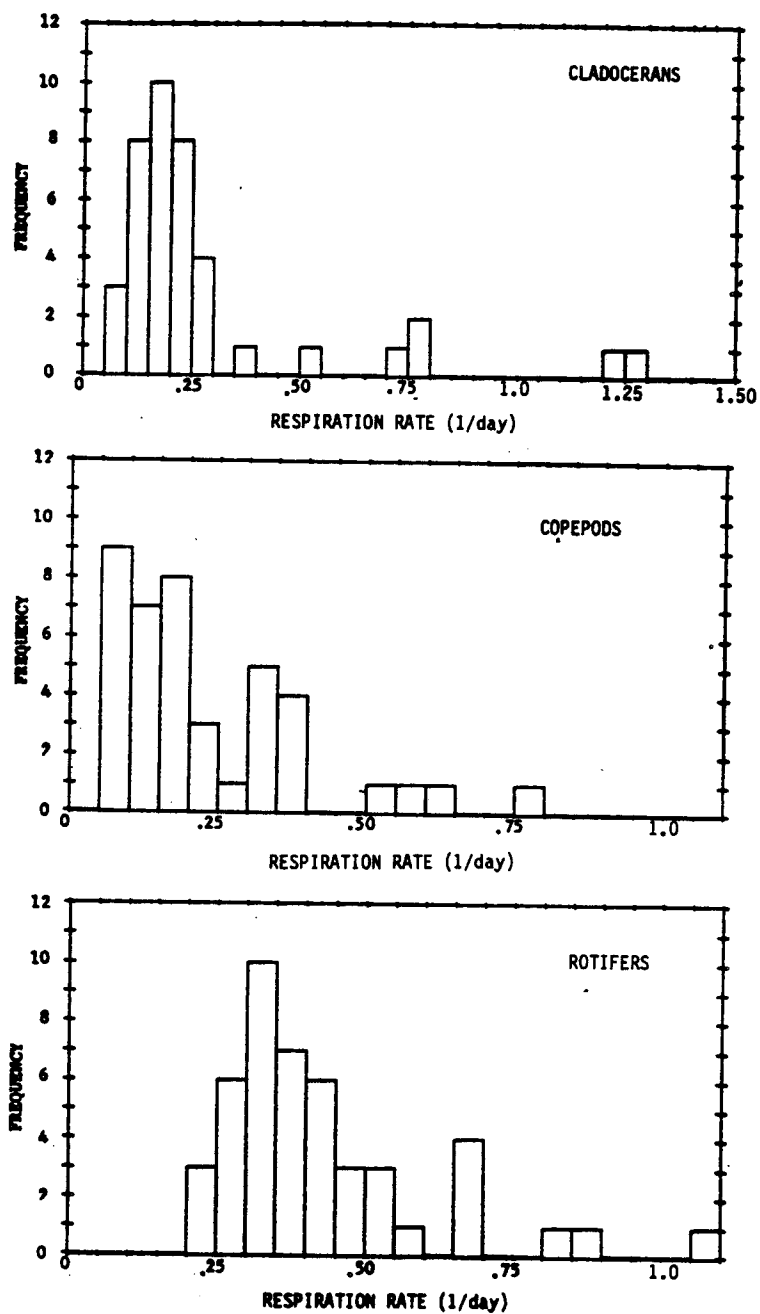
FIGURE 7-6. Frequency histograms of zooplankton respiration
rates (from Leidy and Ploskey, 1980).

$$C_j = \frac{g_j}{E_j} \qquad (7\text{-}44)$$

where C_j = total consumption rate for predator group j, 1/time

g_j = growth rate for predator group j, 1/time

E_j = assimilation efficiency for predator group j

When different assimilation efficiencies are used for different food items, consumption rates are generally calculated directly for each food item and combined with the food specific assimilation efficiencies to determine net growth (as discussed in Section 7.3.3).

7.6 SUMMARY

Zooplankton are typically modeled as a biomass pool using the same mass balance approach used for nutrients, phytoplankton, and other constituents.
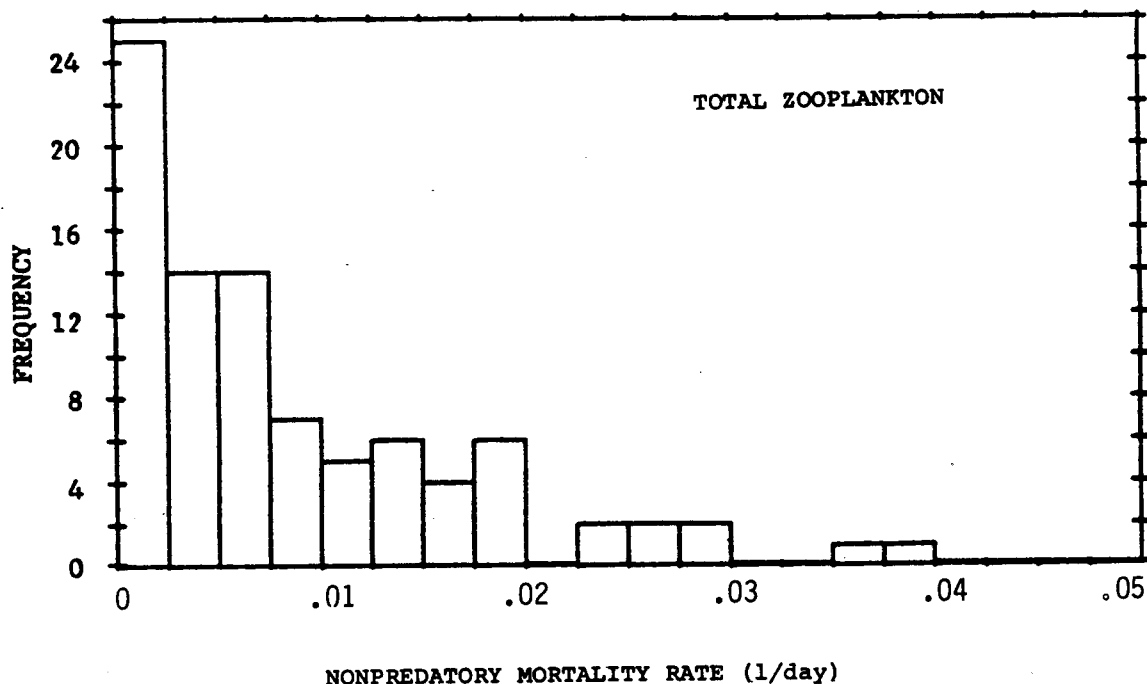

Figure 7-7. Frequency histogram of nonpredatory mortality rates for zooplankton (from Leidy and Ploskey, 1980).

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The simplest models lump all zooplankton into a single group, while more complex models distinguish between different feeding types or different taxonomic groups.

Zooplankton dynamics depend on growth, reproduction, respiration, excretion, predation, and nonpredatory mortality. However, these processes are not generally measured in the field for a specific model application since: 1) many of them are difficult or impossible to measure directly; 2) the rates depend on environmental conditions (e.g., temperature), ecological conditions (e.g., food supply and predator densities), and the species composition of the zooplankton, all of which change continually with time; and 3) the fluxes depend largely on the zooplankton densities, which may vary by orders of magnitude over a seasonal cycle.

As a result, many of the model coefficients must be determined by model calibration rather than by measurement. Model constructs must be relied upon to describe the effects of different factors on these processes. Literature values from laboratory experiments are useful for establishing reasonable ranges of the process rates and coefficients. However, specific experimental results are difficult to apply directly since experiments typically use a single species rather than the species assemblages represented in models, and since experimental conditions may not represent conditions in the field.

Most models include formulations to describe the effects of temperature on all process rates. Food density effects on growth and consumption are typically modeled using saturation kinetics similar to those used for phytoplankton. Respiration and mortality rates are most commonly modeled as first-order losses, although a few models use more complicated formulations which include the effects of other factors, for example, crowding effects. Since few models include higher trophic levels such as fish, predatory mortality is typically treated in a simplistic manner.

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